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Elevated haplotypes frequencies reveal similarities for selection signatures in Western and Russian Simmental populations

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Abstract

This paper shows a straightforward, but surprisingly effective approach to detect genomic regions of importance, illustrated on two Simmental cattle populations. Medium density genomic data of 42 German/Austrian (denoted as “Western“) and 38 Russian Simmental cattle were used to identify the most frequent haplotypes within the two populations. The haplotypes were defined as non-overlapping segments of ten single nucleotide ploymorphisms (SNP). The phasing was done with the SHAPEIT software, with a follow up analysis of haplotypes using the GHap package. Despite the low sample size a number of high frequency haplotypes could be identified accross the whole genome. The identified genes residing direcly in these high frequency haplotypes were extremely relevant for the dual purpose Simmental cattle. A large part of these genes influenced growth rate and carcass traits, others were relevant for the milk production. A smaller proportion was connected to the reproduction, immune system and cellular processes, with indirect influence on production traits.

Keywords: cattle, genome architecture, haplotype analysis, Simmental

Introduction

Haplotypes are chromosomal segments inherited from a single parent, as a result high genetic linkage that keeps the nucleotides within these segments tightly

together. Consequently, the haplotypes could be treated as a more complex form of genetic variant, but with similar utilization possibilities.

Haplotypes could be used, similarly to single nucleotide polymorphisms (SNP), to determine genetic distances between populations, draw associations between haplotypes and traits of interest, identify deleterious variants for disorders, enhancing inbreeding and admixture analyses. A more common use of haplotype based analyses is to detect selective sweeps to identify genomic regions and genes that are important to evolution of the respective species or breeds (Sabeti et al., 2002; Voight et al., 2006; Utsunomiya et al., 2013). Haplotypes with major beneficial effects could be also used to enhance the results of genomic selection.

One of the most popular dual-purpose cattle breed in Russia is the Simmental, with the second largest population after the Holstein cattle, with 96.5 thousand recorded cows in 271 herds and 31 regions (Dunin et al., 2017). The desire to improve the milk production properties in the Russian Simmental population led to imports of related breeds, with increased tendencies from the second half of the 19th century. The herd book of Simmental breed in Russia (USSR) was approved in 1926. From the 1950's for the next 30 years, there was a periodic sire's delivery mainly from Austria, Switzerland, Germany and Hungary. Their offspring, according to the results of the sires' evaluation by the type traits (conformation traits) and the productivity trend, showed well-expressed meat qualities in comparison with milk features. A similar structure was observed between domestic and foreign Simmental populations in Russia. Since the late 1990s and the beginning of the 2000s, European (Western) Simmental livestock was imported, creating a large population of foreign origin in Russia (Sharkaeva, 2013). This required using of sires with the relevant genetic values. Use of the Holstein breed to improve the milk production traits also occurred in both populations.

Currently, the breeding purpose of Russian Simmental is the ratio 60/40 for milk and meat traits, while the German-Austrian population ratio is 38/16/46, respectively, for milk, meat and fitness. Regarding to this, the study for genetic determination of the Simmental population structure in Russia from the point of genomic data is important. The study of mutations caused by the selection pressure is a useful approach for determining the common breeding direction and adjusting the breeding objectives in Simmental breed on the continent. Determination of the genomic variants will make it possible to clarify the patterns associated with milk and meat production traits, which in turn will be taken into account in the development of the genomic evaluation program in Russian Simmental cattle.

Therefore, the aim of this study was to screen two populations of Simmental cattle in order to identify the genomic locations of the most prevalent haplotypes, including any functional genes residing in these regions that could be accounted in the breeding program in the future.

Materials and methods

For the purposes of this paper the Western Simmental cattle means animals with Austrian or German origin. The Russian Simmental population includes animals that have a common national breeding program and own genealogical structure from

1950s to present. The sperm samples from sires were provided by the AI stations located in European part of Russia.

Genomic DNA was extracted using the Nexttec™ isolation kit (Nexttec Biotechnology GmbH, Germany). The original data consisted of 42 Simmental bulls of Western and 38 bulls of Russian origin, genotyped with the Illumina BovineSNP50 v2 chip. A follow up quality control was performed removing animals with SNP missingness more than 10%, as well as SNPs with missingness of more than 10% or minor allele frequency less than 1%. After the filtering process 41 animals and 40,525 SNPs remained in the Western Simmental, and 36 animals and 41,594 SNPs in the Russian Simmental population.

The PLINK 1.9 software (Chang et al., 2015) was used for data processing and quality control. The initial haplotypes were generated with the SHAPEIT software (O'Connell et al., 2014) using default settings. The haplotypes were further dissected to non-overlapping windows of 10 SNPs using the GHap package (Utsunomiya et al., 2016) in R programming language.

The haplotype frequencies were plotted against the starting position for both populations and compared visually. The highest haplotype frequencies at each chromosome without an explicit threshold were examined in detail using the NCBI database using the UMD 3.1.1 reference assembly. Special attention was given to the genomic regions showing elevated frequencies for the same haplotypes in the Simental cattle of both Western and Russian origin.

Results and discussion

The average size of explored regions was 0.245 Mb with standard deviation of 0.209 Mb. In case there was more than one haplotype with elevated frequency directly connected to each other, these were examined as one region. This was especially the case of BTA27, where multiple haplotype blocks identified a region of 1.6 Mb. In other chromosomes, even the longest connected haplotype blocks were up to 0.527 Mb.

In general, the identified haplotypes showed remarkable affinity to identify regions with protein coding genes. The identified regions, their frequencies in the respective population and the full list of protein coding genes are shown in Table 1. The most relevant findings are highlighted in the further discussion. In case there was no haplotype of outstanding frequency on a particular chromosome, this chromosome was omitted from the list.

On BTA1 the haplotype in the same region was found for both populations, containing the SOX14 gene that regulates embryonic development (Arsic et al., 1998). A gene of the same family, SOX17 on BTA14, was identified to affect growth and calving ease (Pausch et al., 2011).

On BTA2 both TRIM63, SLC30A2 are involved in the metabolism of zinc in the body. Notably SLC30A2, also known as Zinc Transporter 2 (ZNT2) plays a role in secreting zinc into milk (Chowanadisai et al., 2006), which in turn affects the cow performance and health (Cope et al., 2009).

On BTA3 the KCNA10 gene is related to potassium metabolism (Lang et al., 2000), involved in a wide range of functional and structural functions.

The genomic region on BTA5 around 56-60 Mb shows elevated haplotype frequencies for both Western and Russian Simmental cattle. The highest frequency in this gene rich region was observed to be 0.83 at the 56.6 Mb in the Russian Simmental. At the edge of the most frequent haplotype is the STAT6 gene, previously associated with carcass and weight traits in cattle (Rincon et al., 2009). The other gene in the haplotype is LRP1, controlling biosynthetic and endocytic trafficking of neuronal prion proteins (Parkyn et al., 2008), including cellular signaling and lipid homeostasis.

On BTA6, the only gene residing in the most frequent haplotype was COX7B2, previously connected to reproductive traits (Randhawa et al., 2014). Further, the COX7B2 is paralog (i.e. a homologous gene that is a result of duplication event before speciation) to the COX7B, involved in the mitochondrial respiratory chain.

An another outstanding haplotype only in the Western Simmental population was in the 39 Mb region of BTA6, including the DCAF16 and LCORL genes, associated with growth and carcass traits (Takasuga, 2016; Zhang et al., 2016; Han et al., 2017).

On BTA10 in both the Western and Russian Simmental cattle there was a major haplotype within the MCC gene, but this gene is without an apparent importance in cattle.

On BTA11 the 3 Mb region in Russian Simmental holds a frequent haplotype containing a large number of genes. In cattle, the most important seems to be the ANKRD23, which was differentially expressed in cows with lower fertility (Moore et al., 2016) and COX5B, also involved in mitochondrial respiratory chain (similarly to genes detected on BTA6), which is connected among others to APT supply to the muscle (Lehnert et al., 2007).

On BTA12 the most frequent haplotype in Western Simmental cattle, with only a low frequency in the Russian population, contained five genes with different functions. From the production perspective, PARP4 influenced carcass weight in Hanwoo cattle (Edea et al., 2018), but also contributed to the environmental adaptation via DNA repair mechanisms (Edea et al., 2014). RNF17 was associated with fatty acid composition in Nelore cattle (Lemos et al., 2016), growth traits in Hanwoo cattle (Edea et al., 2018) and pigs (Puig-Oliveras et al., 2014). MPHOSPH8 was up regulated in atretic follicles in cattle (Hatzirodos et al., 2014). ATP12A was connected to APT mechanisms and high altitude adaptation in goats (Wang et al., 2016).

On BTA13, only a single haplotype was over 50% frequency in the Western Simmental cattle, highlighting a gene rich region. Among the listed genes, the most relevant was DLGAP4, influencing processed ham quality in Italian pig populations (Fontanesi et al., 2017), MYL9 involved in the muscle development, tenderness and texture (Cui et al., 2012), positively selected in Angus cattle (Pérez O'Brien et al., 2014), NDRG3 connected to marbling score (Seong et al., 2016) and SAMHD1 involved in immune response.

Table 1. The list of genomic regions and protein coding genes within the most frequent haplotypes in the Western and Russian Simmental cattle

BTA[a]	Start position[b]	End position[b]	Frequency Western Simmental[c]	Frequency Russian Simmental[c]	Genes
1	132.37	132.618	0.512	0.597	SOX14
2	127.626	127.655	0.512	0.666	TRIM63, SLC30A2
3	32.989	33.018	0.426	0.687	KCNA10
5	56.625	56.699	0.457	0.722	STAT6, LRP1
6	66.897	67.17	0.817	0.653	COX7B2
6	38.689	39.216	0.744	-[d]	DCAF16, LCORL
10	0.496	0.52	0.854	0.708	MCC
11	2.691	3.14	-[d]	0.625	CNNM4, ANKRD23, SEMA4C, FAM178B, COX5B, ACTR1B, ZAP70
12	36.599	37.11	0.549	-[d]	MPHOSPH8, PARP4, CENPJ, RNF17, ATP12A
13	66.179	66.66	0.51	-[d]	DLGAP4, MYL9, TGIF2, SLA2, NDRG3, TLDC2, SAMHD1, RBL1
14	29.444	29.894	-[d]	0.528	NKAIN3, GGH, TTPA, YTHDF3
15	24.14	24.177	0.598	0.525	NCAM1
17	35.494	35.601	0.762	0.708	-
19	56.541	56.594	0.585	0.361	SAP30BP, RECQL5, SMIM5, SMIM6, MYO15B
20	22.195	22.293	0.829	0.742	-
21	57.723	57.765	0.64	0.701	SLC24A4
27	4.948	6.592	0.548	0.333	DEFB variants, GPM6A

[a] BTA - *Bos Taurus* autosome; [b] Positions in mega bases; [c] If there was more than one haplotype in the same region, this is their average frequency; [d] Haplotype frequency low, thus it does not stand out within the population.

On BTA14 the genomic region around 29 Mb contained a frequent haplotype in the Russian population. The entire genomic region is of immense interest to growth related traits (Bolormaa et al., 2011). Also, NKAIN3, TTPA from this high frequency haplotype were associated to carcass and meat quality traits in cattle (Ramayo-Caldas et al., 2014; Sharma et al., 2014).

On BTA17, there were no genes found the highest frequency haplotype around 35 Mb at BTA17 of both breeds. Interestingly, the haplotypes region was flanked by IL2 and IL21, with a potential role in bovine tuberculosis prevention (Endsley et al., 2009). The 49 Mb region contained a region with increased haplotype frequency specific for the Russian population, with the TMEM132D gene connected to milk composition (Poulsen et al., 2015).

On BTA19, the region with highest haplotype frequency in Western Simmental cattle was around 57 Mb, overlapping with a QTL region related to udder health (Wu et al., 2015). The same haplotype region had an elevated frequency also in the Russian Simmental cattle, although the frequency was only about 36% compared to 58% in the Western population.

On BTA20 in both Western and Russian Simmental cattle there were haplotypes with elevated frequencies around 22.2 Mb. Interestingly, there was no gene present in this region. A haplotype with 66% frequency was detected, however, in the Russian population just upstream at 23.3 Mb, containing the MIER3 gene, connected to cattle fertility (Nayeri and Stothard, 2016) and survival (Raven et al., 2014).

On BTA21 the most prominent haplotype in both populations contained the SLC24A4 gene, which was connected to pigmentation related traits (Sulem et al., 2007), but also fertility in cattle (Nayeri et al., 2016).

The most frequent haplotypes on BTA27 overlap only partially in the Western and Russian Simmental population. This region contains surprisingly high number of uncharacterized genes, some of which are denoted as protein coding. In addition, there are a large number of genes from the Defensin (DEFB) family, related to immunity and regulation of inflammation. The GPM6A is also within these haplotypes, connected to udder health (Goldammer et al., 2004), with the whole region appears to be relevant to mastitis resistance in cattle.

Conclusions

Genomic regions with high frequencies of identical haplotyes were identified in Western and Russian Simmental populations. The high haplotype frequencies suggest that selection is acting in these regions. Even when the identified haplotype regions were narrow, they contained genes with remarkable relevance to the Simmental population, confirming the general suitability of the approach.

The functions of identified genes within the regions affect cellular regulation, milk production, but predominantly carcass and weight traits, which is well in line with the breeding goal of the dual purpose Simmental cattle.

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References

Arsic, N., Rajic, T., Stanojcic, S., Goodfellow, P.N., Stevanovic, M. (1998) Characterisation and mapping of the Human SOX14 Gene. Cytogenetics and Cell Genetics, 83 (1-2), 139-146. DOI: https://dx.doi.org/10.1159/000015149

Bolormaa, S., Porto Neto, L.R., Zhang, Y.D., Bunch, R.J., Harrison, B.E., Goddard, M.E., Barendse, W. (2011) A genome-wide association study of meat and carcass traits in Australian cattle. Journal of Animal Science, 89 (8), 2297-2309. DOI: https://dx.doi.org/10.2527/jas.2010-3138

Chang, C.C., Chow, C.C. Laurent, Tellier, C.A.M., Vattikuti, S., Purcell, S.M., Lee, J.J. (2015) Second-Generation PLINK: Rising to the challenge of larger and richer datasets. GigaScience, 4 (7). DOI: https://dx.doi.org/10.1186/s13742-015-0047-8

Chowanadisai, W., Lönnerdal, B., Kelleher, S.L. (2006) Identification of a mutation in SLC30A2 (ZnT-2) in women with low milk zinc concentration that results in transient neonatal zinc deficiency. Journal of Biological Chemistry, 281 (51), 39699-39707. DOI: https://dx.doi.org/10.1074/jbc.M605821200

Cope, C.M., Mackenzie, A.M., Wilde, D., Sinclair, L.A. (2009) Effects of level and form of dietary zinc on dairy cow performance and health. Journal of Dairy Science, 92 (5), 2128-2135. DOI: https://dx.doi.org/10.3168/jds.2008-1232

Cui, H.X., Liu, R.R., Zhao, G.P., Zheng, M.Q., Chen, J.L., Wen, J. (2012) Identification of differentially expressed genes and pathways for intramuscular fat deposition in pectoralis major tissues of fast-and slow-growing chickens. BMC Genomics, 13 (213). DOI: https://dx.doi.org/10.1186/1471-2164-13-213

Dunin, I.M., Amerkhanov, K.A., Safina, G.F., Knyazeva, T.A., Shcheglov, M.E., Zaitceva, O.N., Mukhin, A.E., Bogolyubova, L.P., Pronin, A.V. (2017) Ezhegodnik po Plemennoj Rabote v Molochnom Skotovodstve v Hozyajstvah Rossijskoj Federacii (2016 god). Moskva: Izdatel'stvo FGBNU VNIIplem (in Russian).

Edea, Z., Dadi, H., Kim, S.W., Park, J.H., Shin, G.H., Dessie, T., Kim, K.S. (2014) Linkage disequilibrium and genomic scan to detect selective loci in cattle populations adapted to different ecological conditions in Ethiopia. Journal of Animal Breeding and Genetics, 131 (5), 358-366. DOI: https://dx.doi.org/10.1111/jbg.12083

Edea, Z., Jeoung, Y.H., Shin, S.S., Ku, J., Seo, S., Kim, I.H., Kim, S.W., Kim, K.S. (2018) Genome-wide association study of carcass weight in commercial Hanwoo cattle. Asian-Australasian Journal of Animal Sciences, 31 (3), 327-334. DOI: https://dx.doi.org/10.5713/ajas.17.0276

Endsley, J.J., Waters, W.R., Palmer, M.V., Nonnecke, B.J., Thacker, T.C., Jacobs, W.R., Larsen, M.H., Hogg, A., Shell, E., McAlauy, M., Capinosh Scherer, C.F., Coffey, T., Howard, C.J., Villareal-Ramos, B., Stes, D.M. (2009) The calf model of immunity for development of a vaccine against tuberculosis. Veterinary Immunology and Immunopathology, 128 (1), 199-204. DOI: https://dx.doi.org/10.1016/j.vetimm.2008.10.312

Fontanesi, L., Schiavo, G., Gallo, M., Baiocco, C., Galimberti, G., Bovo, S., Russo, V., Buttazzoni, L. (2017) Genome-wide association study for ham weight loss at first salting in Italian large white pigs: towards the genetic dissection of a key trait for dry-cured ham production. Animal Genetics, 48 (1), 103-107. DOI: https://dx.doi.org/10.1111/age.12491

Goldammer, T., Kata, S.R., Brunner, R.M., Kühn, C., Weikard, R., Womack, J.E., Schwerin, M. (2004) High-resolution comparative mapping between human chromosomes 4 and 8 and bovine chromosome 27 provides genes and segments serving as positional candidates for udder health in cattle. Genomics, 84 (4), 696-706. DOI: https://dx.doi.org/10.1016/j.ygeno.2003.12.003

Han, Y.J., Chen, Y., Liu, Y., Liu, X.L. (2017) Sequence variants of the LCORL gene and its association with growth and carcass traits in Qinchuan cattle in China. Journal of Genetics, 96 (1), 9-17.

Hatzirodos, N., Hummitzsch, K., Irving-Rodgers, H.F., Harland, M.L., Morris, S.E., Rodgers, R.J. (2014) Transcriptome profiling of granulosa cells from bovine ovarian follicles during atresia. BMC Genomics, 15 (40). DOI: https://dx.doi.org/10.1186/1471-2164-15-40

Lang, R., Lee, G., Liu, W., Tian, S., Rafi, H., Orias, M., Segal, A.S., Desir, G.V. (2000) KCNA10: A novel ion channel functionally related to both voltage-gated potassium and CNG cation channels. American Journal of Physiology. Renal Physiology, 278 (6), F1013-1021. DOI: https://dx.doi.org/10.1152/ajprenal.2000.278.6.F1013

Lehnert, S.A., Reverter, A., Byrne, K.A., Wang, Y., Nattrass, G.S., Hudson, N.J., Greenwood, P.L. (2007) Gene expression studies of developing bovine longissimus muscle from two different beef cattle breeds. BMC Developmental Biology, 7 (95). DOI: https://dx.doi.org/10.1186/1471-213X-7-95

Lemos, M.V.A., Chiaia, H.L.J., Berton, M.P., Feitosa, F.L.B., Aboujaoud, C., Camargo, G.M.F., Pereira, A.S.C., Albuquerque, L.G., Ferrinho, A.M., Mueller, L.F., Mazalli, M.R., Furlan, J.J.M., Carvalheiro, R., Gordo, D.M., Tonussi, R., Espigolan, R., Medeiros de Oliveira Silva, R., Nunes de Oliveira, H., Duckett, S., Aguilar, I., Baldi, F. (2016) Genome-wide association between single nucleotide polymorphisms with beef fatty acid profile in Nellore cattle using the single step procedure. BMC Genomics, 17 (213). DOI: https://dx.doi.org/10.1186/s12864-016-2511-y

Moore, S.G., Pryce, J.E., Hayes, B.J., Chamberlain, A.J., Kemper, K.E., Berry, D.P., McCabe, M., Cormican, P., Lonergan, P., Fair, T., Butler, S.T. (2016) Differentially expressed genes in endometrium and corpus luteum of Holstein cows selected for high and low fertility are enriched for sequence variants associated with fertility. Biology of Reproduction, 94 (1). DOI: https://dx.doi.org/10.1095/biolreprod.115.132951

Nayeri, S., Sargolzaei, M., Abo-Ismail, M.K., May, N., Miller, S.P., Schenkel, F., Moore, S.S., Stothard, P. (2016) Genome-wide association for milk production and female fertility traits in Canadian dairy Holstein cattle. BMC Genetics, 17 (75). DOI: https://dx.doi.org/10.1186/s12863-016-0386-1

Nayeri, S., Stothard, P. (2016) Tissues, metabolic pathways and genes of key importance in lactating dairy cattle. Springer Science Reviews, 4 (2), 49-77. DOI: https://dx.doi.org/10.1007/s40362-016-0040-3

O'Connell, J., Gurdasani, D., Delaneau, O., Pirastu, N., Ulivi, S., Cocca, M., Traglia, M., Huang, J., Huffman, J.E., Rudan, I., McQuillan, R., Fraser, R.M., Campbell, H., Polasek, O., Asiki, G., Ekoru, K., Hayward, C., Wright, A.F., Vitart, V., Navarro, P., Zagury, J.F., Wilson, J.F., Toniolo, D., Gasparini, P., Soranzo, N., Sandhu, M.S., Marchini, J. (2014) A general approach for haplotype phasing across the full spectrum of relatedness. PLOS Genetics, 10 (4), e1004234. DOI: https://dx.doi.org/10.1371/journal.pgen.1004234

Parkyn, C.J., Vermeulen, E.G.M., Mootoosamy, R.C., Sunyach, C., Jacobsen, C., Oxvig, C., Moestrup, S., Liu, Q., Bu, G., Jen, A., Morris, R.J. (2008) LRP1 controls biosynthetic and endocytic trafficking of neuronal prion protein. Journal of Cell Science, 121 (6), 773-783. DOI: https://dx.doi.org/10.1242/jcs.021816

Pausch, H., Flisikowski, K., Jung, S., Emmerling, R., Edel, C., Götz, K.U., Fries, R. (2011) Genome-wide association study identifies two major loci affecting calving ease and growth-related traits in cattle. Genetics, 187 (1), 289-297. DOI: https://dx.doi.org/10.1534/genetics.110.124057

Pérez O'Brien, A.M., Utsunomiya, Y.T., Mészáros, G., Bickhart, D.M., Liu, G.E., Van Tassell, C.P., Sonstegard, T.S., Da Silva, M.V.B., Garcia, J.F., Sölkner, J. (2014) Assessing signatures of selection through variation in linkage disequilibrium between taurine and indicine cattle. Genetics, Selection, Evolution: GSE, 46 (19). DOI: https://dx.doi.org/10.1186/1297-9686-46-19

Poulsen, N.A., Rybicka, I., Larsen, L.B., Buitenhuis, A.J., Larsen, M.K. (2015) Short communication: genetic variation of riboflavin content in bovine milk. Journal of Dairy Science, 98 (5), 3496-3501. DOI: https://dx.doi.org/10.3168/jds.2014-8829

Puig-Oliveras, A., Ballester, M., Corominas, J., Revilla, M., Estellé, J., Fernández, A.I., Ramayo-Caldas, Y., Folch, J.M. (2014) A co-association network analysis of the genetic determination of pig conformation, growth and fatness. PloS One, 9 (12), e114862. DOI: https://dx.doi.org/10.1371/journal.pone.0114862

Ramayo-Caldas, Y., Fortes, M.R.S., Hudson, N.J., Porto-Neto, L.R., Bolormaa, S., Barendse, W., Kelly, M., Moore, S.S., Goddard, M.E., Lehnert, S.A., Reverter, A. (2014) A marker-derived gene network reveals the regulatory role of PPARGC1A, HNF4G, and FOXP3 in intramuscular fat deposition of beef cattle. Journal of Animal Science, 92 (7), 2832-2845. DOI: https://dx.doi.org/10.2527/jas.2013-7484

Randhawa, I.A.S., Khatkar, M.S., Thomson, P.C., Raadsma, H.W. (2014) Composite selection signals can localize the trait specific genomic regions in multi-breed populations of cattle and sheep. BMC Genetics, 15 (34). DOI: https://dx.doi.org/10.1186/1471-2156-15-34

Raven, L.A., Cocks, B.G., Hayes, B.J. (2014) Multibreed genome wide association can improve precision of mapping causative variants underlying milk production in dairy cattle. BMC Genomics, 15 (62). DOI: https://dx.doi.org/10.1186/1471-2164-15-62

Rincon, G., Farber, E.A., Farber, C.R., Nkrumah, J.D., Medrano, J.F. (2009) Polymorphisms in the STAT6 gene and their association with carcass traits in feedlot cattle. Animal Genetics, 40 (6), 878-882. DOI: https://dx.doi.org/10.1111/j.1365-2052.2009.01934.x

Sabeti, P.C., Reich, D.E., Higgins, J.M., Levine, H.Z.P., Richter, D.J., Schaffner, S.F., Gabriel, S.B., Platko, J.V., Patterson, N.J., McDonald, G.J., Ackerman, H.C., Campbell, S.J., Altshuler, D., Cooper, R., Kwiatkowski, D., Ward, R., Lander, E.S. (2002) Detecting recent positive selection in the human genome from haplotype structure. Nature, 419 (6909), 832-837. DOI: https://dx.doi.org/10.1038/nature01140

Seong, J., Yoon, H., Kong, H.S. (2016) Identification of microRNA and target gene associated with marbling score in Korean cattle (Hanwoo). Genes & Genomics, 38 (6), 529-538. DOI: https://dx.doi.org/10.1007/s13258-016-0401-y

Sharkaeva, G. (2013) Cattle import in Russian Federation and results of this using. Molochnoe i Myasnoe Scotovodstvo, 8, 18-20. (in Russian).

Sharma, A., Dang, C.G., Kim, K.S., Kim, J.J., Lee, H.K., Kim, H.C., Yeon, S.H., Kang, H.S., Lee, S.H. (2014) Validation of genetic polymorphisms on BTA14 associated with carcass trait in a commercial Hanwoo population. Animal Genetics, 45 (6), 863-867. DOI: https://dx.doi.org/10.1111/age.12204

Sulem, P., Daniel, F. Gudbjartsson, S., Stacey, N., Helgason, A., Rafnar, T., Magnusson, K.P., Manolescu, A., Karason, A., Palsson, A., Thorleifsson, G., Jakobsdottir, M., Steinberg, S., Palsson, S., Jonasson, F., Sigurgeirson, B., Thorisdottir, K., Ragnarsson, R., Benediktsdottir, K.R., Aben, K.K., Kiemeney, L.A., Olafsson, J.H., Gulcher, J., Kong, A., Thorsteinsdottir, U., Stefansson, K. (2007) Genetic determinants of hair, eye and skin pigmentation in Europeans. Nature Genetics, 39 (12), 1443-1452. DOI: https://dx.doi.org/10.1038/ng.2007.13

Takasuga, A. (2016) PLAG1 and NCAPG-LCORL in livestock. Animal Science Journal, 87 (2), 159-167. DOI: https://dx.doi.org/10.1111/asj.12417

Utsunomiya, Y.T., Pérez O'Brien, A.M., Sonstegard, T.S., Van Tassell, C.P., Carmo, A.S., Mészáros, G., Sölkner, J., Garcia, J.F. (2013) Detecting loci under recent positive selection in dairy and beef cattle by combining different genome-wide scan methods. PLOS ONE, 8 (5), e64280. DOI: https://dx.doi.org/10.1371/journal.pone.0064280

Utsunomiya, Y.T., Milanesi, M., Utsunomiya, A.T.H., Ajmone-Marsan, P., Garcia, J.F. (2016) GHap: An R package for genome-wide haplotyping. Bioinformatics, 32 (18), 2861-2862. DOI: https://dx.doi.org/10.1093/bioinformatics/btw356

Voight, B.F., Kudaravalli, S., Wen, X., Pritchard, J.K. (2006) A map of recent positive selection in the human genome. PLOS Biology, 4 (3), e72. DOI: https://dx.doi.org/10.1371/journal.pbio.0040072

Wang, X., Liu, J., Zhou, G., Guo, J., Yan, H., Niu, Y., Li, Y., Yuan, C., Geng, R., Lan, X., An, X., Tian, X., Zhou, H., Song, J., Jiang, Y., Chen, Y. (2016) Whole-genome sequencing of eight goat populations for the detection of selection signatures underlying production and adaptive traits. Scientific Reports, 6, 38932. DOI: https://dx.doi.org/10.1038/srep38932

Wu, X., Lund, M.S., Sahana, G., Guldbrandtsen, B., Sun, D., Zhang, Q., Su, G. (2015) Association analysis for udder health based on SNP-Panel and sequence data in Danish Holsteins. Genetics Selection Evolution, 47 (50). DOI: https://dx.doi.org/10.1186/s12711-015-0129-1

Zhang, W., Li, J., Guo, Y., Zhang, L., Xu, L., Gao, X., Zhu, B., Gao, H., Ni, H., Chen, Y. (2016) Multi-strategy genome-wide association studies identify the DCAF16-NCAPG region as a susceptibility locus for average daily gain in cattle. Scientific Reports, 6. DOI: https://dx.doi.org/10.1038/srep38073